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# Sexual Competition Among Male Blue Crab, *Callinectes sapidus*

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**Abstract.** Experiments and field data on blue crab, *Callinectes sapidus*, from mid-Chesapeake Bay between 1991 and 1994 were used to test whether large males have advantages over small males in accessing females and in sperm competition. In the field, large males were paired more often, especially with large, more fecund females. However, the variance in the relationship between male and female size in mating pairs was high, suggesting that mating with large females may not be the primary determinant of male reproductive success. Large males had proportionately longer chelipeds, which may provide an advantage in aggressive interactions for females or in struggles to control females. Previous work indicates that sperm competition may occur in blue crabs and that ejaculate size may influence a male's ability to compete during sperm competition. Large males stored more seminal fluid and spermatophores and passed a larger volume of ejaculate to each mate than did small males. Ejaculate volume averaged 47% of a male's stored supply. However, ejaculate volume increased with the duration of copulation but decreased with successive matings, such that males needed about 15 days between matings to pass similar-sized ejaculates to successive mates. Pre-copulatory mate guarding may serve as a time to replenish ejaculate contents, and thus its duration also influences a male's performance in sperm competition.

## Introduction

Competition among males for reproductive females is one of the most important forces in the evolution of mating behavior (Andersson, 1994). Males compete for access to females when receptive females are numerically, spatially, or temporally limited in relation to males (Trivers, 1972; Emlen and Oring, 1977; Clutton-Brock and Parker, 1992). Males can also compete by means of sperm competition: when females copulate with more than one male and sperm from the different males compete in the female reproductive tract for unfertilized eggs (Parker, 1970; Smith, 1984). Mate guarding is a behavior that males use to compete for access to females as well as in sperm competition (Grafen and Ridley, 1983; Smith, 1984). Pre-copulatory mate guarding often occurs when females are sexually receptive for only a limited period; it ensures that guarding males will have access to a receptive female (Parker, 1974; Grafen and Ridley, 1983). Post-copulatory mate guarding prevents rival males from mating with the inseminated female; therefore, guarding males control access to a female's eggs (Parker, 1970). Mate guarding is widespread among taxa, suggesting that it can enhance mating success in males facing competition from other males (Ridley, 1983; Smith, 1984).

In many species among different taxa, large males have advantages over smaller rivals both in competition for access to females and in sperm competition (Thornhill and Alcock, 1983; Andersson, 1994). Large males often dominate smaller males during aggressive interactions for females (Stein, 1976; Ridley and Thompson, 1979; Ward, 1983; Berrill and Arsenault, 1984), and more easily obtain and physically control females (Berrill and Arsenault, 1982; Carvacho, 1989; Snedden, 1990; Lee and Seed, 1992). As a result, large males can have higher fertilization rates because they more often mate with large, more fecund females (Stein, 1976; Ridley and Thompson, 1985; Forbes *et al.*, 1992; Stevens *et al.*, 1993). The advantages of large male size often result in positive assortative mating; a positive correlation between male and female size in mating pairs (Crespi, 1989). Males may respond to an

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increased risk of sperm competition by guarding for longer durations (Sherman, 1983; Wilber, 1989; Jablonski and Kaczanowski, 1994) or by passing larger ejaculates (Svard and Wiklund, 1989; Gage, 1991; Eady, 1995; Gage and Barnard, 1996), which displace more of a previous inseminator's sperm or prevent dilution by a subsequent inseminator. Compared to small males, large males of some species have greater stores of ejaculate contents (Kwei, 1978; Wilber, 1987; LaMunyon and Eisner, 1993; Pitnick, 1996), pass larger ejaculates even after a number of sequential matings (Markow *et al.,* 1978), and avoid being displaced during mating (Borgia, 1981; Howard and Kluge, 1985; Elwood *et al.,* 1987). Preventing displacement may allow large males to guard or copulate longer, and can result in passing larger ejaculates (McLain, 1980; Svard and Wiklund, 1988).

Male blue crab, *Callinectes sapidus,* exhibit both pre- and post-copulatory mate guarding, suggesting that they may compete both for access to females and in sperm competition. Males may mate several times (although the number of possible matings is undetermined) within a mating season, whereas females mate immediately after their final (pubertal) molt to maturity (Van Engel, 1958; Millikin and Williams, 1980) and usually with a single male (Jivoff, 1997). Thus, theoretically, competition for access to females is expected because at any one time more males than females are available to mate (Clutton-Brock and Parker, 1992). Male blue crab use their chelipeds in both aggressive interactions for females and struggles with females for physical control (Teytaud, 1971; Smith, 1992). In other species, longer chelipeds help large males out-compete smaller males for access to females (Berrill and Arsenault, 1984; Snedden, 1990; Lee and Seed, 1992; Moriyasu and Comeau, 1996; Paul and Paul, 1996), as suggested by mating patterns in the field that show paired males to be larger than unpaired males (Harvey, 1990; Stevens *et al.,* 1993) and reveal some degree of size-assortative mating (Adams *et al.,* 1985; Reid *et al.,* 1994).

Recent experimental and field evidence indicates that sperm competition may occur in blue crab, because some females (about 12%) remate within several days after their final molt, storing both ejaculates in their entirety such that sperm from both males may have equal access to the unfertilized eggs (Jivoff, 1997). As a result, males may enhance their fertilization rate by preventing rivals from mating with the female or by ejaculating greater numbers of sperm in the female relative to that of other males (Parker, 1984). Thus, sperm competition in blue crab can be argued to favor those males that spend a longer time guarding and pass more ejaculate to each female. Indeed, male blue crab increase the duration of post-copulatory mate guarding when the sex ratio is male-biased, and they pass larger ejaculates in the presence of other males or of previous ejaculates in the female (Jivoff, 1997).

The following paper (1) shows evidence from field data for an advantage of large male size during competition for access to females; (2) experimentally shows how male size, mating history, and copulation duration influence ejaculate volume, which may influence a male's ability to compete during sperm competition; and (3) discusses how competition among males for access to females may interact with sperm competition to influence male mating success.

## Materials and Methods

Research was carried out at the Smithsonian Environmental Research Center (SERC) on the Rhode River, a subestuary of Chesapeake Bay, in Maryland (38°51′N, 76°32′W) from mid-June through late September, 1991–1994. All crabs used in experiments were collected in the field. Seines and trawls were sometimes used, but most specimens were taken with a dip net, 2–3 times per week, from the sides of commercial pound nets (length 150–200 m) stretched between vertical posts near the mouth of the Rhode River. Crabs were transported to SERC, measured (see below), separated by sex, maintained in floating field cages in the Rhode River, and fed fish daily until used in experiments.

Variables recorded from field-captured crabs included sex, paired status (pre-copulatory, post-copulatory, copulating, or unpaired), molt stage (see below), sexual maturity (juvenile, pre-pubertal or pre-molt, mature), carapace width (CW; distance, in millimeters, between the tips of the lateral spines), chelae spread (distance, in millimeters, between the tips of the chelipeds when fully extended laterally, 1994 only), and the number and position of missing limbs. Molt stage was determined by examining the propodus on the fifth appendage for evidence of epidermal retraction and color variation and, for recently molted crabs, the relative hardness of the newly formed carapace (Van Engel, 1958). Pre-pubertal females have a triangular, darkened abdomen, whereas adults have a semicircular abdomen. Pre-molt females were designated as follows: early/$D_0$ (9–10 days pre-molt); early-mid/$D_1$ (7–8 days pre-molt); mid/$D_2$ (5–6 days pre-molt); mid-late/$D_3$ (3–4 days pre-molt); and late/$D_4$ (1–2 days pre-molt) (Drach, 1939). Males were designated sexually mature according to the criteria of Van Engel (1990): the second pleopods lay within the first pleopods (intromittent organs); the penes were inserted into the second pleopods; and the abdomen easily pulled away from the sternum. I used only mature, intermolt males that possessed both chelipeds and that were missing not more than one walking leg, a condition that does not affect mating behavior or mating success (Smith, 1992). Crabs in experiments

were never held in field cages for more than 1 week and were never reused.

Male blue crabs store spermatophores and seminal fluid in paired vas deferentia (Cronin, 1947; Johnson, 1980). Each vas deferens is connected to an external pleopod, through which seminal fluid and spermatophores are passed to one of the female's two spermathecae (Cronin, 1947; Hartnoll, 1968). No difference was found between the weight of material males store in each vas deferens (paired $t = 0.306$, df = 10, $P = 0.766$) or pass through each pleopod (paired $t = 0.276$, df = 158, $P = 0.783$) (Jivoff, 1995). Thus, the amount of seminal fluid and spermatophores that males stored in their reproductive tracts and passed to females was weighed using the following protocol. One (randomly assigned) pleopod from each male was removed with dissecting scissors at least 24 h prior to the experiment. After the male copulated once in an experimental pool, each vas deferens was weighed (nearest 0.01 g). The vas deferens with the intact pleopod transferred the normal amount of ejaculate, but the vas deferens lacking a pleopod ("unmated") transferred none. As a result, ejaculate weight was calculated as the difference between the weight of the unmated and mated vas deferentia. The proportion of available material passed was also calculated by dividing the weight of the ejaculate by that of the unmated vas deferens. The surgical procedure proved effective because neither spermatophores nor seminal fluid were lost after pleopod removal, and no difference was found between the calculated weight of the ejaculate passed and the measured weight of the spermathecal contents (paired $t = 0.704$, df = 42, $P = 0.485$). The relationships of both seminal stores and ejaculate size to male size were determined with linear regression.

To test whether ejaculate weight served as a measure of the amount of sperm transferred to the female, the relationship between the number of spermatophores within the ejaculate and the weight of the ejaculate was determined. The seminal fluid portion of the ejaculate hardens over time and most of the spermatophores accumulate in a single, large mass at the distal end of the spermathecae, but some are incorporated within the seminal fluid matrix (Johnson, 1980). One spermatheca from each of 29 females was weighed (nearest 0.01 g) and then cut into four equal-sized sections (bisecting longitudinally and again transversely) using dissecting scissors. For a random quarter, the hardened ejaculate was scraped from the inside wall of the spermatheca and the seminal fluid was teased apart under a dissecting microscope to count the spermatophores. Maximum lengths of 25 spermatophores in each ejaculate were measured (to the nearest micrometer). Linear regression was used to determine the relationship between ejaculate weight and both the number of spermatophores and the average length of spermatophores, and between male size and the average length of spermatophores.

The relationship between female size and the weight of the empty spermathecae was determined both as a measure of the sperm storage capacity of females and to estimate the weight of the spermathecal tissue in the total weight of mated spermathecae. Pre-molt females ($n = 27$) were isolated from males, and after their pubertal molt their spermathecae were weighed (nearest 0.01 g). The relationship between average spermathecal weight and female carapace width (pre-molt and adult calculated separately) was determined with linear regression. The weight of the spermathecal tissue was calculated using the appropriate regression equation. In all of the statistical comparisons of the contents of female spermathecae described below, the weight of the spermathecal tissue is removed.

The effect of male and female size on the contents of female spermathecae in the field was estimated using one-way ANOVA to determine how paired male size, adult female size, and female spermathecal contents varied among years. Tukey multiple comparisons tests were used to identify significant differences between years. The spermathecae of the adult females (both paired and unpaired) from each collection date were weighed (nearest 0.01 g). For each year, the relationship between the size of adult females and the total contents of their spermathecae was determined using linear regression. The slopes and elevations of the statistically significant regressions were compared using the $t$ test (Zar, 1984).

*Pool experiments*

All of the experiments described below were performed in plastic pools (2 m in diameter and 0.3 m deep). Each pool contained about 10 cm of sand and was filled with water from the Rhode River. The pools were constantly aerated and the water was completely changed every 1–2 days. Test salinities matched that of the Rhode River (5–10 ppt), and water temperatures were about 5°C below that of the Rhode River, varying little among pools (22°–27°C). Crabs were exposed to the ambient light:dark cycle (14:10). A 0.5-m-high "fence" of hardware cloth was placed around the inside perimeter of each pool and covered with a piece of plywood. The cover protected crabs from terrestrial predators (*e.g.,* raccoons), direct sunlight, and elevated water temperatures. Pools were monitored several times daily for the presence of courtship, copulation, and both types of mate guarding. Crabs in pools were fed two to three frozen, previously crushed, mussels (*Mytilus* sp.) daily.

*Male mating history*

The effect of male size and number of previous copulations (mating history) on the weight of ejaculate passed

to females during subsequent copulations was determined. Each of six males in each of three size categories (small, <135 mm CW; medium, 135–145 mm CW; and large, >145 mm CW) were mated successively with three virgin females of similar size (90-110 mm CW), randomly assigned among males. The range of male size spanned that of paired males in the field. To ensure that males were previously unmated, they were collected early in the season before any natural matings were observed in the field. Each male was randomly assigned to a test pool, and all males received their first female on the same day. Males were provided successive females within 24 h of their previous copulation; however, differences in female molt stage produced differences in the time between matings (mating interval). Regardless of when males were capable of mating again, mating actually occurred only when the female was ready to molt. After mating, each female's spermathecae were weighed (nearest 0.01 g). The ability of males to replenish their ejaculate contents between matings was estimated by calculating the difference between the weight of ejaculate passed in one mating and that passed in the previous mating. Repeated-measures ANOVA with paired contrasts tested the total weight of both spermathecae from each female as a function of male size category after treatment variances were examined with the Bartlet test. The relationship between ejaculate replenishment and mating interval was determined with linear regression.

*Duration of copulation*

The effect of male size and copulation duration on the amount of ejaculate passed to virgin females was determined with a two-factor design of male size (small, medium, and large) and copulation duration (1, 2, 4, 8 h, or uninterrupted, about 12 h). The male size categories were the same as in the mating history experiment (see above). The copulation durations and the start of copulation were designated on the basis of the following observations. The male turns the newly molted female over so his sternum rests on hers; copulation begins after he inserts his pleopods into her vulvae, and may last for 12 h (Van Engel, 1958). Each replicate ($n = 2$) included one mating pair for each treatment combination of male size category and copulation duration. To control the start of each copulation, I provided males with pre-molt females that I predicted would molt within several hours. If a female did not molt on the day she was first introduced, then she was isolated from the male and presented to him the following day, when it was possible to observe the start of copulation. Copulations were interrupted after the designated time by physically separating the mating pair. Each female was sacrificed and her spermathecae were weighed (nearest 0.01 g). Interactive effects of male size and copulation duration on the combined weight of both spermathecae were analyzed with two-way ANOVA after testing for homogeneity of variances with the Bartlet test. A Tukey multiple-comparisons test identified significant differences among treatments. The field and experimental data were analyzed using Systat (SYSTAT, 1992). In the text, means are presented with their standard errors (±1 SE).

## Results

*The size of males in the field*

The size range of sexually mature males overlapped in each of four years: 1991, 105–179 mm CW; 1992, 95–184 mm CW; 1993, 103–204 mm CW; and 1994, 110–

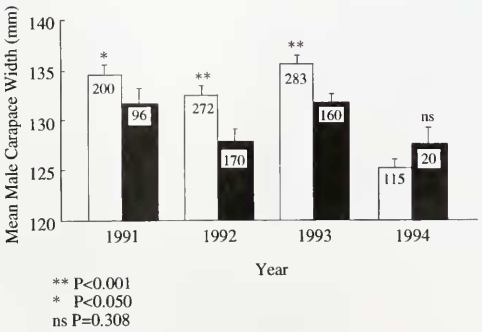


**Figure 1.** Mean carapace width of pre-copulatory mate-guarding males (open bars) and unpaired mature males, in the intermolt stage only (dark bars), captured in the field during each year of the study. Numbers inside each bar are sample sizes. Vertical bars are 1 standard error.

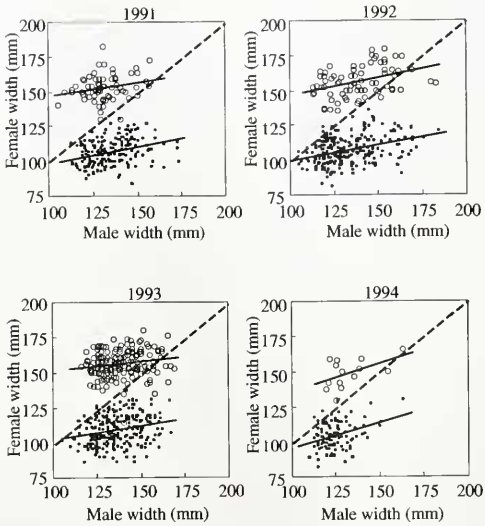


**Figure 2.** Relationship between guarding-male carapace width and pre-molt (■) and adult (○) female carapace width in mate-guarding pairs captured in the field during each year of the study. The dashed line in each graph indicates where the male and female size are equal. The regression lines for pre-copulatory mate-guarding pairs are as follows: 1991—$Y = 0.24X + 74.44$, $r^2 = 0.099$, $P < 0.001$, $n = 200$; 1992—$Y = 0.22X + 77.11$, $r^2 = 0.123$, $P < 0.001$, $n = 272$; 1993—$Y = 0.20X + 82.31$, $r^2 = 0.064$, $P < 0.001$, $n = 283$; 1994—$Y = 0.36X + 59.46$, $r^2 = 0.104$, $P < 0.001$, $n = 114$. The regression lines for post-copulatory mate-guarding pairs are as follows: 1991—$Y = 0.19X + 127.69$, $r^2 = 0.051$, $P = 0.069$, $n = 66$; 1992—$Y = 0.25X + 121.88$, $r^2 = 0.142$, $P = 0.001$, $n = 73$; 1993—$Y = 0.12X + 139.24$, $r^2 = 0.026$, $P = 0.035$, $n = 174$; 1994—$Y = 0.39X + 96.35$, $r^2 = 0.263$, $P = 0.061$, $n = 14$.

164 mm CW. In three years, the mean CW of paired males was significantly larger than that of unpaired males, but in 1994 there was no significant difference (Fig. 1). In each year, large males were more often paired with large pre-molt females (Fig. 2). Large males were also more often paired with large adult females in post-copulatory mate-guarding pairs in 1992 and 1993 (Fig. 2). Paired males were typically larger than pre-molt females but smaller than their adult female partners. However, in each year, male size explained little (2%–26%) of the variation in the size of paired pre-molt or adult females. A significantly positive allometric relationship ($\beta = 1.148$, $P < 0.001$) occurred between male CW and the distance between the tips of male chelipeds when fully extended laterally (chelae spread), indicating that large males have proportionately longer chelipeds than small males (Fig. 3).

### *The size of males and the weight of ejaculates*

The number of spermatophores present in the ejaculate increased significantly with ejaculate weight ($Y = 0.613X + 2.49$, $r^2 = 0.332$, $n = 29$, $P = 0.001$) (Fig. 4); however, no relationship was found between male CW and spermatophore size ($n = 29$, $P = 0.446$) or between ejaculate weight and spermatophore size ($n = 29$, $P = 0.592$). The amount of seminal fluid and spermatophores stored in the vas deferens both before ($Y = 0.04X - 2.40$, $r^2 = 0.263$, $n = 335$, $P < 0.001$) and after ($Y = 0.03X - 1.92$, $r^2 = 0.202$, $n = 335$, $P < 0.001$) one mating increased with male size (Fig. 5). Furthermore, the size-related increase in the weight of seminal products stored before mating was significantly larger than that after mating ($t = 3.12$, df = 669, $P < 0.002$), indicating that large males pass more ejaculate than do small males. Weights of female spermathecae contents also indicate that the weight of ejaculate stored by females increased with the size of their mate ($Y = 0.015X - 0.484$, $r^2 = 0.096$, $n = 334$, $P < 0.001$). On average, males passed 46.9% (±0.008 SE) of their available ejaculate. The relationships between adult female size and the weight of ejaculate received ($n = 212$, $P = 0.172$), and the proportion of ejaculate received ($n = 212$, $P = 0.10$) were not significant.

### *Contents of female spermathecae in the field*

The weight of empty spermathecae increased with size of pre-molt females (Fig. 6). As compared with small

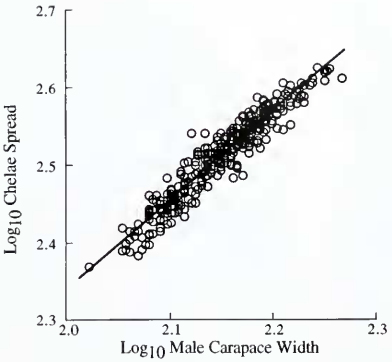


**Figure 3.** Relationship between $\log_{10}$ carapace width and $\log_{10}$ chelae spread among adult male blue crabs. Chelae spread is the distance (in millimeters) between the tips of the chelae when they are extended laterally to 180° from the anterior. The regression line is described by the following equation: $Y = 0.044X + 1.148$, $n = 358$, $r^2 = 0.922$, $P < 0.001$. The slope indicates significant positive allometry $F_{1,356} = 69.90$, $P < 0.001$.

females, large females carried more ejaculate in both spermathecae in 1994 ($Y = 0.003X + 0.043$, $r^2 = 0.052$, $n = 185$, $P = 0.002$), and 1993 ($Y = 0.001X + 0.453$, $r^2 = 0.011$, $n = 389$, $P = 0.04$), but not in 1992 ($n = 171$, $P = 0.136$). The slopes of the regressions in 1994 and 1993 were not significantly different ($t = 1.8$, df = 571, $P > 0.05$); however, in 1993 females had significantly more material stored in their spermathecae than they did in 1994 ($t = 9.4$, df = 572, $P < 0.001$). There were significant differences in the spermathecal contents ($F_{2,742} = 53.24$, $P < 0.001$), paired male size ($F_{2,968} = 36.33$, $P < 0.001$), and adult female size ($F_{2,744} = 11.72$, $P < 0.001$) among years (Fig. 7). Furthermore, the pattern of the differences was consistent among years; the weight of female spermathecal contents was greatest when paired male size and adult female size were the largest (Fig. 7).

*Male mating history*

Male size ($F_{2,15} = 8.96$, $P = 0.003$) and number of previous mates ($F_{2,30} = 5.19$, $P = 0.012$) had a significant effect on the total ejaculate passed to females. Large males passed significantly larger ejaculates to their first ($F_{1,10} = 10.36$, $P = 0.009$), second ($F_{1,10} = 34.29$, $P = 0.0002$), and third females ($F_{1,10} = 5.80$, $P = 0.036$) than did small males (Fig. 8). Large males passed significantly

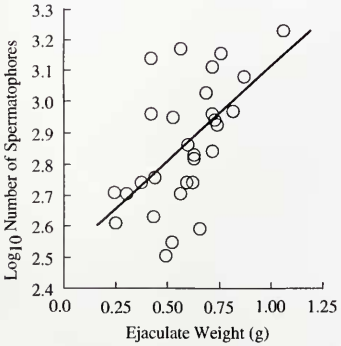


**Figure 4.** Relationship between ejaculate weight and the $\log_{10}$ number of spermatophores contained in the ejaculate. The regression line is described by the following equation: $Y = 0.613X + 2.49$, $r^2 = 0.332$, $P = 0.001$, $n = 29$.

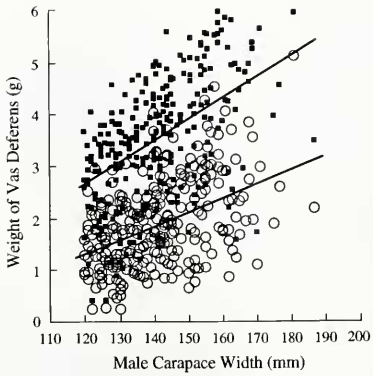


**Figure 5.** Relationship between male carapace width and the weight of ejaculate stored in the vas deferens before (■) and after (○) mating. Males had one pleopod removed before mating. Ejaculate stored before mating was the weight of the unmated (full) vas deferens. Ejaculate stored after mating was the weight of the mated (spent) vas deferens. The equations for the regression lines are as follows: $Y = 0.04X - 2.40$, $r^2 = 0.263$, $P < 0.001$, $n = 335$ (before mating) and $Y = 0.03X - 1.92$, $r^2 = 0.202$, $P < 0.001$, $n = 335$ (after mating). The before-mating slope is larger than the after-mating slope ($t = 3.12$, df = 669, $P < 0.002$).

larger ejaculates to their second mate than did medium-sized males ($F_{1,9} = 16.63$, $P = 0.003$) (Fig. 8). Overall, a significant decrease in the combined weights of both female spermathecae occurred across all three matings ($F_{1,15} = 5.88$, $P = 0.028$). A significant decrease occurred in the weight of large male ejaculates across all three matings ($F_{2,8} = 5.28$, $P = 0.034$), but not in the ejaculate weights of small ($F_{2,12} = 0.996$, $P = 0.398$) or medium ($F_{2,10} = 1.691$, $P = 0.233$) males. Ejaculate replenishment after the first mating (ejaculate weight in mating 2 minus

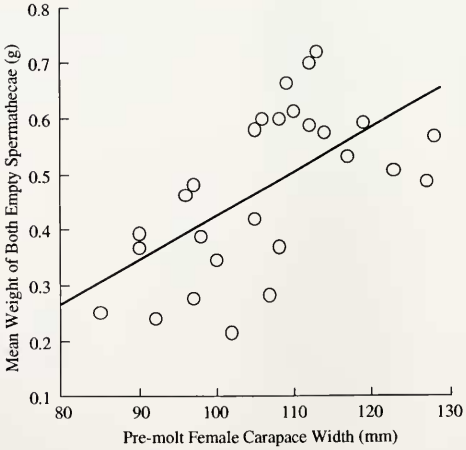


**Figure 6.** Relationship between unmated, pre-molt female carapace width and the mean weight of both empty spermathecae within the female. Females were isolated from males during the pubertal molt to ensure that their spermathecae were empty of male-derived material. $Y = 0.009X - 0.46$, $r^2 = 0.363$, $P = 0.001$, $n = 28$.

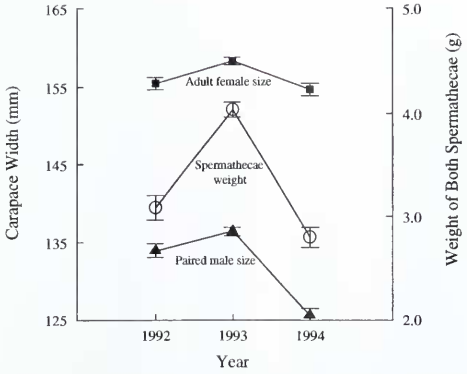


**Figure 7.** Sizes of adult females (■) and paired males (▲) and weight of female spermathecae (○) between 1992 and 1994. Results of Tukey comparison tests for differences between years are as follows: for females—1993 > 1992 ($P = 0.002$); 1993 > 1994 ($P < 0.001$), for males—1993 > 1992 ($P = 0.007$), 1993 > 1994 ($P < 0.001$) and 1992 > 1994 ($P < 0.001$); and for spermathecal contents—1993 > 1992 ($P < 0.001$), 1993 > 1994 ($P < 0.001$) and 1992 > 1994 ($P = 0.005$). Vertical bars are ±1 standard error.

ejaculate weight in mating 1) increased with the interval between the first and second matings (Fig. 9) but not with that between the second and third matings ($n = 19$, $P = 0.588$). The interval between the first and second matings did not differ significantly from the interval between the second and third matings ($t = 1.99$, df = 36, $P = 0.056$).

*Copulation duration*

There was a significant effect of copulation duration ($F_{4,35} = 18.64$, $P < 0.001$) but not male size ($F_{2,35} = 0.544$, $P = 0.585$) on the amount of ejaculate passed to females. The interaction between male size and copulation duration was not significant ($F_{8,27} = 0.403$, $P = 0.909$). Males that copulated without interruption (8–12 h) passed larger ejaculates than males that were interrupted after 1, 2, or 4 h; males that were interrupted after 8 h passed larger ejaculates than males interrupted after 1 or 2 h (Fig. 10). No significant difference was found between the size of ejaculates passed by males that were interrupted after 8 h and that of uninterrupted males (df = 37, Tukey HSD = 0.319).

## Discussion

In the field, paired males were larger than unpaired males in each year except 1994, and there was consistent, positive assortative mating between males and pre-molt females. The discrepancy in the results for 1994 may be the result of cold weather in that year, which retarded the growth of crabs and shortened the mating season. Consequently, the mean size of paired males (see Fig. 7), the size range (54 mm CW) and maximum size (164 mm CW) of sexually mature males was low compared with other years: 1991, 74 mm CW and 179 mm CW; 1992, 89 mm CW and 184 mm CW; 1993, 101 mm CW and 204 mm CW. In blue crab and other crab, males use their chelipeds extensively during inter- and intrasexual interactions that lead to mating success, and the loss of one cheliped is a handicap in competition for females (Smith, 1992; Abello *et al.*, 1994; Paul and Paul, 1996). My results indicate that the chelipeds are proportionately longer in large male blue crab than in smaller ones; this length difference may, as seen in other species (Berrill and Arsenault, 1984; Carvacho, 1989; Homola *et al.*, 1991; Lee and Seed, 1992), provide a reach advantage during pair formation, and aggressive interactions for females, or both. Large males may also have advantages in maintaining their post-copulatory embrace, as indicated by the positive assortative mating with post-molt females in 1992 and 1993, because post-molt females were often larger than their male partner. In other crustaceans, small males often fail to remain paired with females that are larger than themselves (Adams, 1982; Verspoor, 1982; Adams and Greenwood, 1983; Forbes *et al.*, 1992). If female blue crab choose among potential mates, they may, as in other species, prefer large males for more protection from injury during takeover attempts (Smith, 1992) or from predation mortality during the female's soft, post-molt phase (Jivoff, 1997).

In each year, the relationship between male and female size in mating pairs was highly variable, suggesting that factors in addition to body size influence which individu-

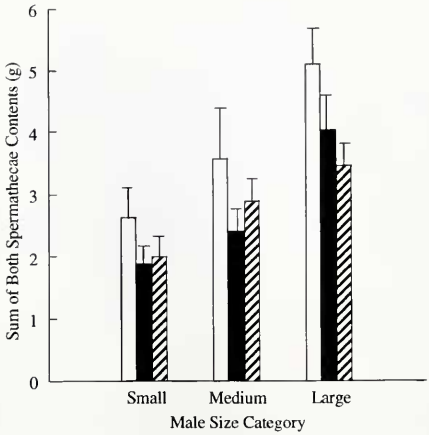


**Figure 8.** Sum of contents of both spermathecae from the first (□), second (■), and third (▨) females mated in succession by males in three size categories. The following are the results of paired contrasts between male size categories: first mating—large *vs.* small ($P = 0.009$), large *vs.* medium ($P = 0.182$), medium *vs.* small ($P = 0.338$); second mating—large *vs.* small ($P = 0.0002$), large *vs.* medium ($P = 0.003$), medium *vs.* small ($P = 0.272$); and third mating—large *vs.* small ($P = 0.036$), large *vs.* medium ($P = 0.359$), and medium *vs.* small ($P = 0.084$). Vertical bars are 1 standard error.

als are paired. In blue crab, a female's fecundity in a single brood increases with size, but the relationship is highly variable (Prager *et al.*, 1990), especially in comparison with other crab species (Hines, 1982). The number of broods female blue crab produce varies seasonally and annually across the geographic range of the species (Chesapeake Bay: Provenzano *et al.*, 1983; Johnson and Hester, 1989; Jones *et al.*, 1990; von Montfrans *et al.*, 1990, South Carolina: Boylan and Wenner, 1993, Florida: Steele and Bert, 1994). Variation in fecundity per brood and

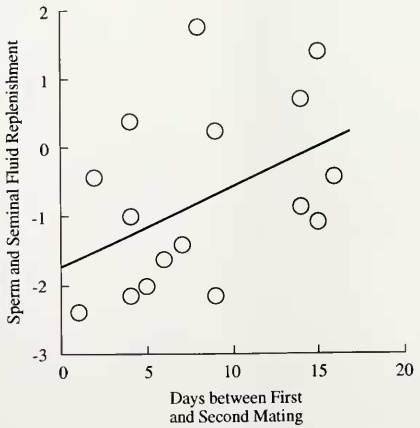


**Figure 9.** Relationship between ejaculate replenishment (total ejaculate passed in mating 2 − total ejaculate passed in mating 1) and the number of days between the matings. The regression equation is as follows: $Y = 0.14X - 2.01$, $r^2 = 0.243$, $n = 16$, $P = 0.038$.

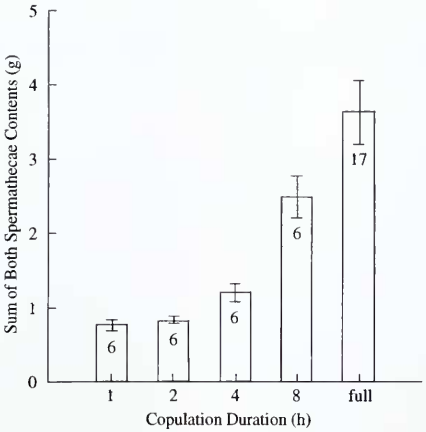


**Figure 10.** Effect of copulation duration on the amount of seminal fluid and spermatophores passed to both spermathecae. Results of a sample of uninterrupted matings (labeled "full") are also included. Numbers inside the bars are sample sizes. The differences are as follows: 4 h > 1 h ($P = 0.04$), 8 h > 1 h ($P < 0.001$), full > 1 h ($P < 0.001$) and 8 h > 2 h ($P = 0.001$), full > 2 h ($P < 0.001$), full > 4 h ($P = 0.014$). Vertical bars are ±1 standard error.

total brood production suggests that the fecundity benefits conferred by large females are uncertain. Female molt stage also influences which individuals are paired by affecting both the ease with which males can establish mate guarding and its duration (Jivoff and Hines, in press). Large females take longer to progress through the final molt cycle than smaller females (Smith, 1997), thus males specializing in large females may mate guard for the longest durations. A simulation model (Jivoff, 1995) shows that male blue crab can enhance their seasonal reproductive success by pairing for shorter durations, implying that late pre-molt females of any size may be preferred over large females in earlier molt stages. Thus, factors that influence both a male's mating frequency and his fertilization rate per female may regulate male mating success in blue crab.

The experimental results indicate that large males pass larger ejaculates to each of their mates than do small males. In the field, females held more material in their spermathecae when large males were more often in mating pairs; this observation also suggests that large males provide females with larger ejaculates. In a variety of other species, large ejaculates ensure that more eggs are fertilized (Gwynne, 1984; Woodhead, 1985; Simmons, 1988; Wiklund *et al.*, 1993) and enhance a male's ability to compete for unfertilized eggs if the female remates (Gromko *et al.*, 1984; Gage, 1991; Lewis and Austad, 1994; Eady, 1995). My field results suggest that large males have access to more unfertilized eggs by means of size-assortative mating, therefore they may enhance their fertilization rate by passing large ejaculates. Previously, I have shown that large ejaculates may provide males with disproportionate access to a female's unfertilized eggs if she remates (Jivoff, 1997). The experimental results indicate that large males pass large ejaculates because they have greater stores of spermatophores and seminal fluid, because they can copulate for at least 8 h, or both. In other species, large males may copulate for longer durations (Ward and Simmons, 1991), because they can resist disruptions and displacement during copulation (Berrill and Arsenault, 1982; Abele *et al.*, 1986; Reid *et al.*, 1994; Hazlett, 1996). I have no size-related measures of copulation duration; however, large male blue crab prevent aggressive displacement by other males during mate guarding (Smith, 1992; Jivoff, 1995) and therefore may copulate longer than small males.

Ejaculates may be costly for males to produce, and the number of sperm per ejaculate may influence a male's paternity, so males should allocate their ejaculates among females, and adjust the size of ejaculates to ensure high levels of paternity (Dewsbury, 1982; Parker, 1990). In a single mating, males passed an average of 47% of their stored seminal products, but when males, especially large ones, mated in rapid succession there was a decrease in the size of their ejaculates. This decrease suggests that one cost of passing consistently large ejaculates is an increase in the time needed to replenish seminal products. One experiment provided an indirect measure of ejaculate

replenishment on the basis of the size of successive ejaculates, but it may also be important to control the time between successive matings. In blue crab and other portunids, replenishment of a male's sperm and seminal fluid may be incomplete if the interval between successive copulations is less than 15 days (see Fig. 9) (Ryan, 1967). In blue crab (Jivoff, 1995) and other crustaceans (Manning, 1980), males respond to increased numbers of competitors with longer periods of pre-copulatory mate guarding. This response ensures a male's access to a female, and by increasing the time between matings, may also provide time for replenishment or build-up of ejaculate supplies. Large ejaculate stores may be an advantage in the presence of rivals because the risk of sperm competition increases, and male blue crab respond to that risk by passing larger ejaculates (Jivoff, 1997). A larger ejaculate may enhance a male's fertilization rate, even if the female remates, because each inseminator's ejaculate appears to have access to the unfertilized eggs (Jivoff, 1997).

Male blue crab compete for access to mates and perhaps, through sperm competition, for the unfertilized eggs of the female. My results suggest that large body size gives a male an advantage in both forms of competition; however, the variability in both the degree of assortative mating and the investment in ejaculate contents by males of different size suggests that male size is but one factor influencing male mating success. Male blue crab appear to have responded to sexual competition with both pre- and post-copulatory mate guarding, therefore the factors that influence the duration of both types of mate guarding may interact to influence male mating success. The results suggest that the time spent in pre-copulatory mate guarding may influence a male's ability to replenish his supply of sperm and seminal fluid, which may, in turn, affect his ability to compete during sperm competition.

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